

The Impact of Pierid Feeding on Seed Production by a Native California Crucifer

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Abstract. Feeding by an inflorescence/infructescence-consuming Pierid, probably *Anthocharis sara stella*, destroyed between 41 and 49% of potential seed output in an isolated stand of the native Sierran Crucifer *Arabis holboellii* var. *pinetorum*. Damage was concentrated on leaders, probably for phenological reasons.

Ever since Hairston, Smith, and Slobodkin (1960) argued that herbivores could not be food-limited because "the world is green," ecologists have labored to understand whether and why this should be the case. Several quantitative studies have now appeared on patterns of utilization of Cruciferous hosts by Pierid butterflies. These have revealed complex situations in which both direct and indirect evidence for both intra- and interspecific competition has been adduced. The present paper reports an instance of very intense damage to the developing fruits (siliques) of a native Sierra Nevada Crucifer, *Arabis holboellii* Hornem. var. *pinetorum* (Tides.) Roll. The case is of special interest because the entire plant population could be censused and the pattern of damage determined with considerable precision.

The plants were located in dry Jeffrey Pine—Incense Cedar—White Fir forest with *Ceanothus* and *Ribes* understory, along the California-Nevada border about 3 km N Verdi, NV (2000 m). They formed a discrete population, with no conspecifics observed in any direction for a distance of 0.75 km. The only other Crucifers found within this circle were four *Lepidium virginicum* var. *pubescens* (Greene) Thell. and several vegetative rosettes of *Rorippa* sp. in a seep. All were undamaged. All *Arabis* were examined on 6 July 1984 and the following data collected: height, phenophase (vegetative, flowering, fruiting), number of intact and missing or damaged siliques per branch. Rarely, damage to the apical portion of the shoot was so severe that the number of missing siliques had to be estimated. Damage estimates are systematically low, because no attempt was made to assess potential reproduction lost by destruction of flowers or buds. The term "leader" used in this paper refers to the central axis which develops first from the rosette. "Branch" refers to products of axillary buds on this axis, which do not bloom until after the "leader" to which

they are attached has done so. Two plants were missing the distal portions of their leaders due to vertebrate (probably rabbit) grazing. The complete results are reported in Table 1.

If all siliques are treated as equal, total loss of reproductive potential in the population was 41%. For the 13 plants which suffered damage, this increases to 49.1%. Two plants—one the largest in the stand—suffered no losses. Damage was much less severe on side branches. On plants sustaining damage, the ratio of intact to damaged or lost siliques was 43:116 for leaders, 78:1 for branches. Branches were almost inevitably much shorter than leaders and were produced later. Some branching may be in response to damage, but undamaged plants also branch. Several

Table 1. Census of *Arabis* plants at a forest site near Verdi, NV, 6 July 1984.

Height of leader (cm)	Number of intact siliques, by branch	Number of damaged or missing siliques, by branch	Height of leader (cm)	Number of intact siliques, by branch	Number of damaged or missing siliques, by branch
76	22	0	35.5	6	4
	3	0		2	0
	4	0		3	0
	3	0	20.3	0	13
	5	0		3+	0
				1	0
51	7	8	23	3	12
	5+ ¹	0	(two leaders)		
	2+	0		3	0
30.5	1+	9		2	0
25	(tallest branch) — leader missing ²			6	0
	1	0		0	10
	2	1		2	0
60	0	8		2	0
	11	0		3	0
	16	0	50	16	2
23	(tallest branch) — leader missing ²		36	0	14
	4	0		4+	0
	5	0	21	6	0
25	1	16	35	2	8
38	1	12			
	3	0			
	3	0			
	4	0			
			Vegetative rosettes: 35 plants.		
			Total Siliques:	167	117

¹+indicates still in flower.

²rabbit damage.

branches were still in flower, but no leaders were. Presumably the difference in damage to leaders vs. branches reflects phenophase when the females were ovipositing—not a “preference” for one or the other.

Although no larvae were found at the site, frass was present and the only infructescence-feeding Pierid common in the area is *Anthocharis sara stella* W. H. Edwards. This is a red-egg species (Shapiro, 1981a) which normally lays only one egg per inflorescence, and the larvae cannibalize both eggs and smaller larvae (Shapiro, unpubl.), so that it is very rare to find more than one larva on a leader though there may be several on a large, bushy, multi-stemmed plant. The difference in damage to leaders vs. branches would only be apparent if the leaders were themselves sufficient to support the full development of the larva. This seems to be the case, since nearly all leaders had a significant number of “left-over,” undamaged siliques and the amount of damage was sufficient, based on rearing experience, to carry the larvae through to pupation.

One plant had twin basal rosettes, each with its own leader. The intact: damaged or lost ratios for the siliques were 3:12 and 0:10 for the leaders and 11:0 and 7:0 for their respective branches.

No information is available on seed quality or germinability from leaders vs. branches. Siliques are almost invariably smaller on branches than in corresponding positions on leaders.

Discussion

Virtually all Pierid-Crucifer studies find a conspicuous “edge effect,” that is, the impact of the herbivore is disproportionately high on isolated and marginal individuals of the plant and low deep within stands. This is true on weedy Crucifers (Shapiro, 1975, 1981a,b, 1985a) but also on native species (Shapiro, 1981b,c). Any situation in which there is high intrapopulation variance in either survivorship or reproduction is potentially a case of natural selection at work. The “edge effect” results in such a variance, but unless central and peripheral plants differ in a heritable way (such as seed size, translating into dispersability), selection is unlikely to follow. If site (central vs. peripheral) is determined probabilistically, and the consequences of drawing a bad site are catastrophic, the selective result should be the acquisition of anti-herbivory mechanisms by the population as a whole (such as the “false eggs” of some *Streptanthus*, Shapiro, 1981a,c). However, most Pierids are phenological specialists; many require plants in bud or early flower for oviposition. The distribution of damage may then be due to the degree to which the butterflies and plants are “in phase.” If damage is strongly correlated with phenology (Shapiro, 1985b), herbivory may select for earlier or later blooming (if the insect emergence time is predictable, and “all else being equal”), or for a “risk-spreading strategy” with high intrapopulation variance in phenology (if the insect is unpredictable).

In this stand of *Arabis*, the evidence suggests that oviposition was concentrated in a short period of time. In a compact stand contained within 1.5 ha in an open environment easy to search, 86.6% of the plants in the appropriate phenophase were damaged. Subsequent branching may allow at least the larger and more vigorous plants to recoup their losses. Only long-term phenological studies can reveal whether a directional shift in blooming time is to be expected as a result of herbivory.

The distribution of many native montane Crucifers appears superficially similar to the *Arabis* near Verdi: relatively local and isolated populations of moderate to occasionally high density. This may be the historically "normal" context in which ecological and evolutionary phenomena relating to host selection and competition have evolved in the Crucifer-Pierid system. Heavy but spotty damage, strongly affected by the phenology of both butterfly and plant (and thus by weather), may be much more "normal" than the very low levels of damage commonly observed in weedy systems. The searching behavior of females, egg-load assessment, cannibalism and convergence may all be much more explicable under these circumstances than in the more familiar, highly disturbed ones where they are usually studied.

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